

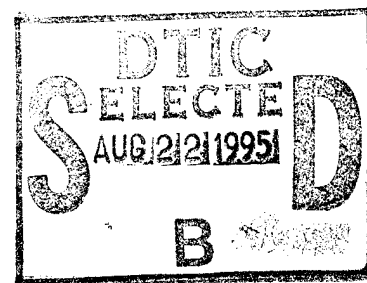
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## *HUMAN ELECTROPHYSIOLOGICAL RESPONSES TO TACTILE STIMULI PRESENTED AT DIFFERENT RATES*

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HUMAN ELECTROPHYSIOLOGICAL RESPONSES TO TACTILE STIMULI  
PRESENTED AT DIFFERENT RATES

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## SUMMARY

Only a few human electrophysiological studies have employed tactile stimulation of the skin. Traditionally, somatosensory evoked potentials (SEPs) have been elicited by punctate electrical stimulation of whole peripheral nerve, bypassing normal transduction mechanisms and precluding comparison with psychophysical measurements. In this report, we show that the small-amplitude response to localized tactile driving at a range of stimulation rates is readily detectable in scalp recordings and is localized to the appropriate scalp region. This holds for measures obtained using either time- or frequency-domain analyses. Furthermore, examination of response entrainment to prolonged vibratory stimulation revealed systematic and reproducible response amplitude changes, having cycle lengths of 20-40 seconds.

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## INTRODUCTION

Traditionally, studies of somatosensory evoked potentials (SEPs) in humans have employed primarily by punctate electrical stimulation of peripheral nerve (e.g., Allison et al. 1989, 1991a, 1991b; Desmedt 1988; Erwin et al. 1987; Larrea et al. 1992). Although responses to electrical shocks have served well to elucidate the neural genesis of these surface-recorded potentials (Allison et al. 1989, 1991a, 1991b, 1992; Desmedt 1988), they have, nevertheless, failed to provide a physiologically meaningful correlate of psychophysically-relevant tactile experience (Rosner and Goff 1967; Sherrick and Cholewiak 1986; Uttal and Cook 1964). Stimuli that engage normal transduction mechanisms, e.g. taps or vibrations delivered to the skin, have been employed in only a few studies (e.g., Franzen and Offenloch 1969; Galambos 1982; Gjerdingen and Tomsic 1970; Hamalainen et al. 1990; Hari 1980; Hashimoto et al. 1988, 1990; Hay and Davis 1971; Huttunen and Homberg 1991; Johnson et al. 1975; Kekoni et al. 1992; Pratt et al. 1980, 1986; Stowell 1975). Because driving of skin mechanoreceptors with vibratory stimuli has proved particularly useful in characterization of the input channels involved in tactile perception, it has been used extensively in psychophysical studies of somatosensation in humans (Gescheider and Wright 1968; Goble and Hollins 1993; Hahn 1968; Hollins et al. 1990). Vibratory input is also useful for exploration of system linearity at progressively higher levels along the somatosensory pathway (Goodwin, John and Darian-Smith 1989; Mountcastle 1984; Namerow et al. 1974; O'Mara et al. 1988). Nevertheless, only a few somatosensory electrophysiological studies to date have employed vibratory tactile stimulation (see McLaughlin and Kelly (1993) for a review). In contrast, a large number of studies employing periodic or oscillatory sensory input can be found in vision (e.g., Bach et al. 1988; Greenlee and Heitger 1988; Ho and Berkeley 1988; Nelson et al. 1984; Regan 1989) and audition (e.g., Galambos et al. 1981; Galambos and Makeig 1988, 1992a, b; Hari et al. 1989; Makeig 1993; Makeig and Inlow 1993; Pantev et al. 1993; Picton et al. 1987).

Previously Galambos and colleagues observed that the intensity of frequency-following responses, or steady-state responses (SSRs), to prolonged auditory tones presented at rates near 40 Hz were enhanced relative to responses elicited by a range of other stimulation rates (10-70 Hz; Galambos et al. 1981). Similar, but very preliminary, studies were conducted in somatosensation, where it was observed that the largest response amplitudes occurred at about 33 Hz (Galambos 1982). Additionally, previous studies of rate effects on somatosensory evoked responses have clearly demonstrated that response amplitude varies inversely with the interval between stimulus presentations (see McLaughlin and Kelly (1993) for a review).

The purpose of this study was to characterize scalp-recorded responses to tactile stimuli presented at different rates. Based on the previous results from auditory and somatosensory studies by Galambos and colleagues, we used two stimulus frequencies: one near 33 Hz and another near 40 Hz. Furthermore,

to examine the effects of stimulus interval on the size of the somatosensory evoked response, stimuli were also presented at rates of 1/sec and 1/10 sec both alone and in combination with more rapid stimuli.

## MATERIALS AND METHODS

### *Subjects*

Five healthy volunteers (3 males, 2 females; mean age = 26.44, s.d. = 4.77) were recruited for participation. Subjects reported having no neurological disorders.

### *Stimulus Parameters*

Mechanical square-wave pulses were delivered to non-hairy skin via a plastic probe connected to the moving coil of an electromechanical vibrator encased in a grounded metal box. Voltage supply to the coil was under computer control. No feedback mechanism was available to ensure that the skin underwent the same degree of indentation with each excursion (Chubbuck 1963). Each stimulus pulse had a 3-msec duration. The stimulus probe diameter was 4 mm for all sessions, except for one session with subject 5 in which a 6.3-cm diameter probe was used. When the smaller probe was used, only the index finger tip was stimulated. The 4-mm diameter probe protruded through a small opening (about 6 mm in diameter) in a circular platform on which the remaining parts of the hand rested. The larger probe—a flat, thin plastic disk—was used to simultaneously stimulate the tips of three fingers (the index, middle and ring).

Stimulus presentation rates were 1/10 sec, 1/sec, or 32.5; a rate of 39 Hz was used in one session with subject 5 (the same session in which the 6-mm diameter probe was employed). Intensity of the target stimulus was set at a fixed, moderate amplitude for the 1/sec and 1/10sec rates. For the rapid rates, stimuli were presented continuously during each run, beginning shortly before the first data collection epoch. At these faster rates, the onset of each recording epoch was associated with a moderate 16dB increase in a single pulse (considered the target stimulus in the rapid-rate condition) within the on-going stream of continuous stimulation. This discontinuity in stimulus amplitude elicits an evoked response that contains the conventional SEP components.<sup>1</sup> Further details about subject participation and stimulus parameters in each of the stimulation conditions is provided in the Results section.

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<sup>1</sup> Using an analogous protocol, Galambos and Makeig (1989) have previously observed short-duration changes in amplitude and phase measurements of frequency-domain data elicited by perturbation of a single pulse within a continuous, periodic train of tone pips (Makeig and Galambos 1989). This change was termed the complex event-related potential, or CERP. Our protocol for stimulation near 33 and 40Hz uses the concept of the CERP in its design; however, only a small number of datasets were explored for the presence of this phenomenon. In most instances, a CERP was indeed in evidence (this finding will not be discussed further).

### *Data collection*

Scalp electrodes were located at 16 International 10/20 sites fixed into a flexible cap (Electro-Cap International). The right earlobe served as reference. Electrooculographic data were recorded at the outer canthi. Bandpass on the Grass amplifiers was 0.1 and 100 Hz; gain for each EEG channel was 50,000. Sampling rates were exactly eight times the stimulus presentation rate for the high rates; at slower rates data were sampled at 260-269 per second. Each epoch consisted of pre- and post-stimulus periods, and the number of epochs collected per run varied according to stimulation rate. Each run lasted approximately 6 minutes.

Subjects wore shielded headphones into which suprathreshold white noise was delivered at a level sufficient to mask sounds produced by the stimulator. Subjects were asked to relax and sit quietly during testing. During some sessions, subjects fixated on a cross-hair placed at eye-level and located approximately four feet in front of them, while in other runs, subjects were asked to close their eyes; these variations were not differentiated in data analysis.

### *Analysis*

Epochs containing large voltages ( $> \pm 90\mu\text{V}$ ) due to eye movements or other artifacts were excluded from analysis. Accepted epochs were averaged across runs, as described in the Results section. In the rapid stimulation conditions, response amplitude and phase (relative to signal onset) were determined using discrete Fourier analysis. These data were converted to the frequency domain by a Fast-Fourier Transform (FFT). Frequency spectra were calculated using the overlap-add periodogram approach applied to response magnitude estimates obtained from FFT analysis.

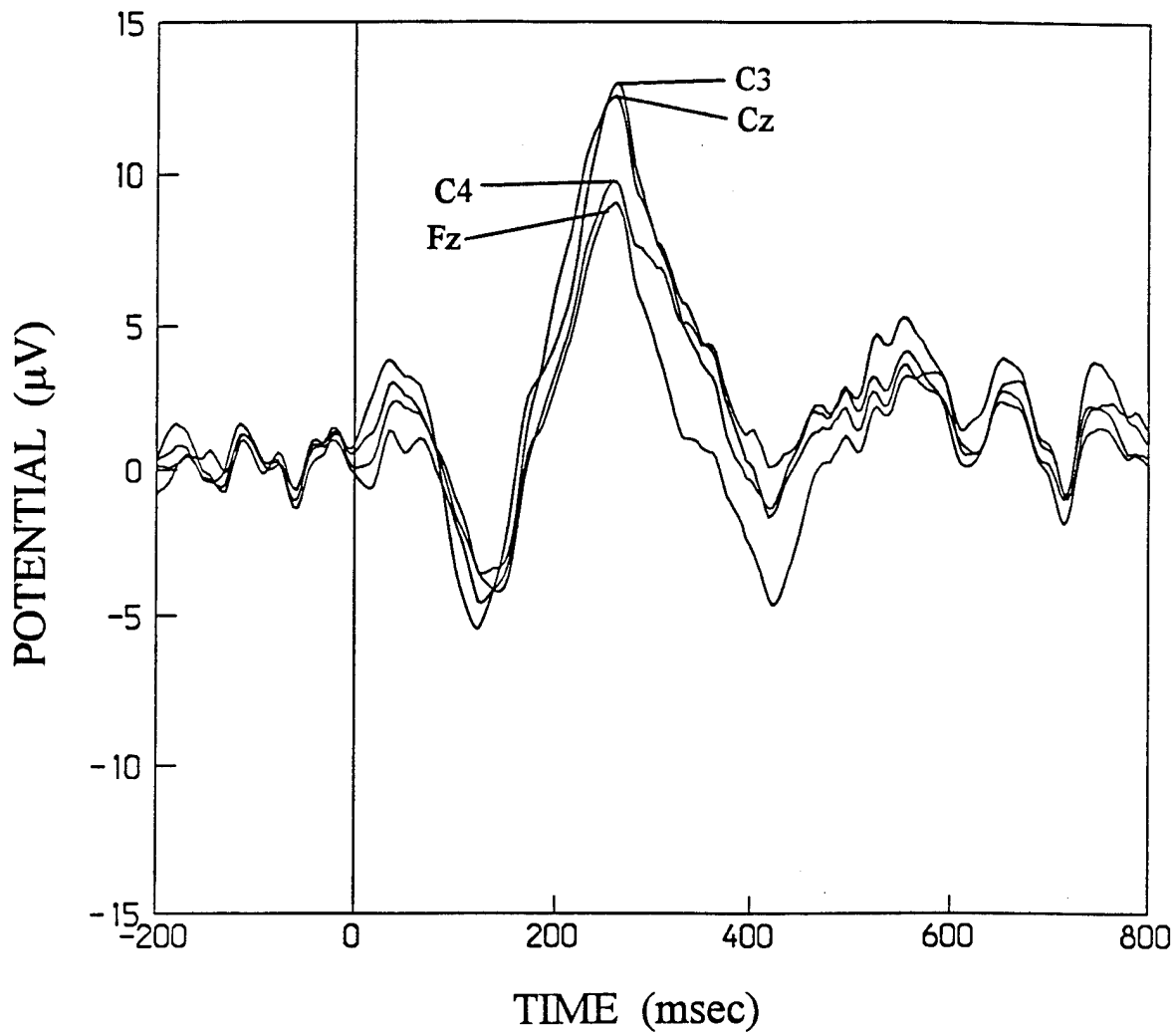
## RESULTS

### *Responses to Stimulation at Slow Rates*

#### General features of the time-domain evoked response

Evoked responses to stimulation of the right index finger at a rate of one stimulus per ten seconds are shown in the time-domain plot of Figure 1. Three peaks were clearly prominent over contralateral scalp at C3, and these could also be distinguished at Cz. An early positive peak appears at about 50 msec, largest at channel C3 which overlies contralateral primary somatosensory cortex (SI). A second peak is negative-going, has an onset at approximately 90 msec, and a maximal value at about 125

**Figure 1.** Scalp-recorded activity evoked by one stimulus per ten seconds. Averaged responses for 13 runs from subjects 1 and 2 (N=435 epochs). Plot shows 200msec of prestimulus activity followed by 800msec of the post-stimulus response. Stimulation was presented to the right index fingertip. Channels are labeled according to the conventional placement standard described by the International 10/20 System.



msec. The largest component is a positive peak at approximately 250 msec, prominent over both contralateral scalp and midline.

The scalp distribution of these components is shown in Figure 2, in which time-domain responses are arranged according to actual scalp locations. One striking feature of these plots is the restricted localization of the early, approximately 50-msec peak to contralateral parietal scalp. The ensuing negative and positive components are more widely distributed. Although, for subject 2, these are clearly largest over contralateral scalp.

Compared with the response components observed at one stimulus per second, evoked response peaks elicited by one stimulus per second are markedly smaller in amplitude and less distinct (Figure 3). In channel C3, two peaks are evident in the 200-250 msec latency range. The second, later peak, although small, may be analogous to the large 250-msec peak prominent at 1/10sec stimulation rates. The first peak appears analogous to the prominence on the ascending limb of the 250-msec component in Figures 1 and 2, and may have become more evident due to the reduction in the size of the 250-msec peak in the 1/sec condition.

#### Amplitude

Comparison of Figures 1 and 3 indicates that evoked responses were largest to stimulation at one presentation per ten seconds. For instance, the base-to-peak amplitude of the small peak at 25-50msec for the 1/10sec result is larger than that of the largest peak obtained at the 1/sec stimulus rate (Cp. Figures 1 and 3).

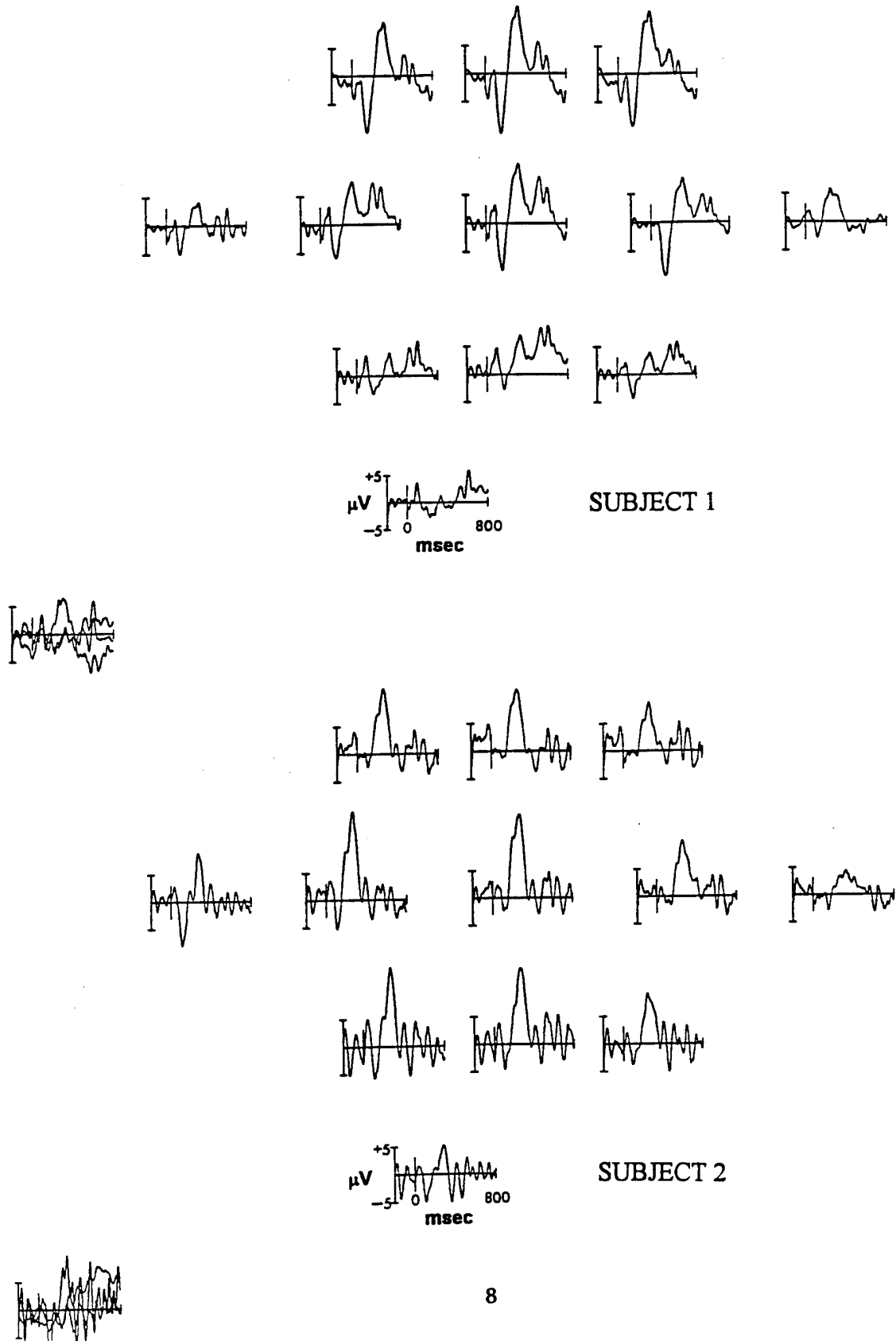
It was also noted that in both the 1/sec and 1/10 sec conditions the response to the first stimulus in each run was well above background EEG level, whereas the responses to the second and subsequent stimuli were indistinguishable from the level of the background EEG (data not shown). This suggests that some degree of habituation occurs even after a 10-second rest period.

#### Topography

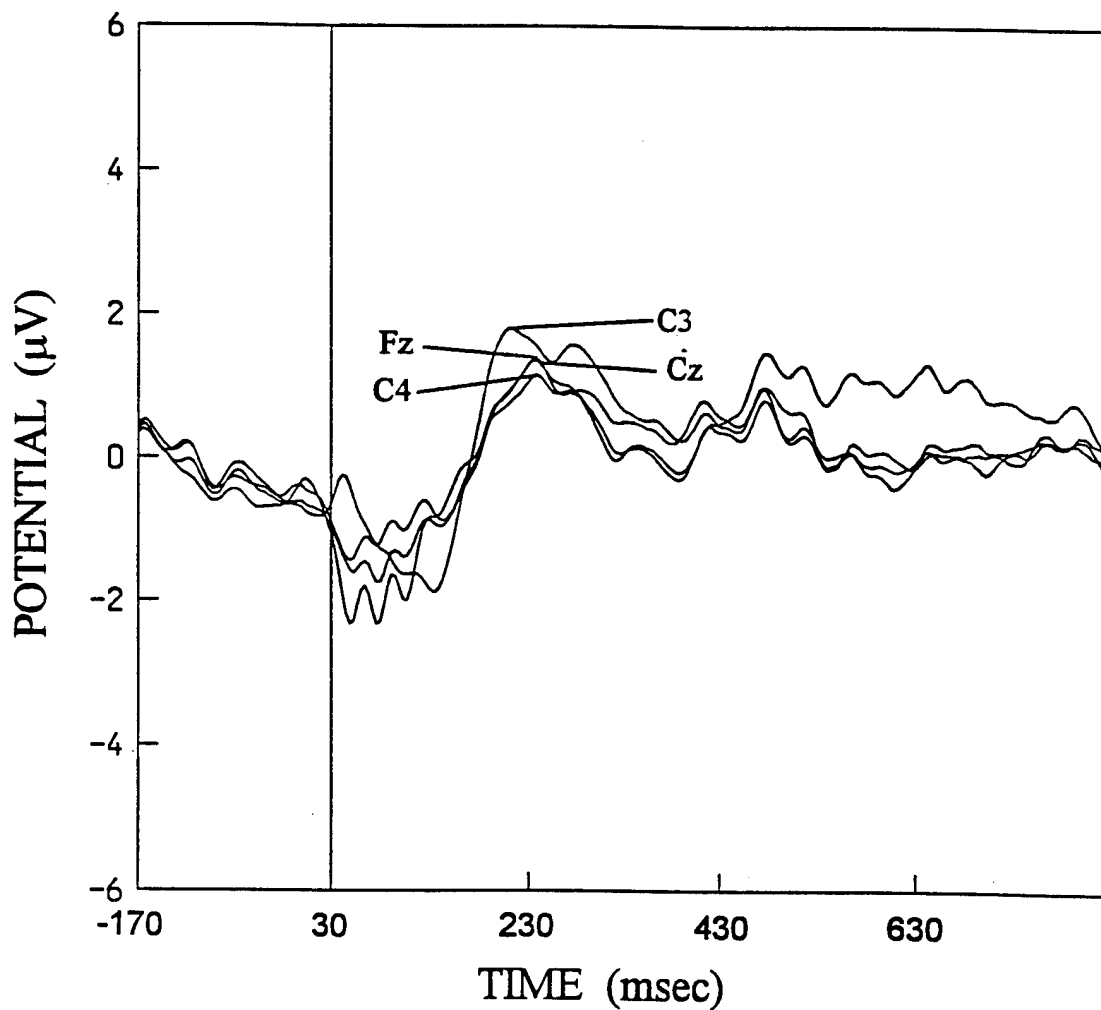
As depicted in Figures 1, 2, and 3, the amplitudes of the prominent components of the evoked response are maximal over contralateral scalp. This finding is shown more clearly in the topographic maps of Figure 4, which were obtained from the same averaged data used for Figure 1. Topographies are shown for the 50-msec (Figure 4A) and 250-msec (Figure 4 B, C) components.



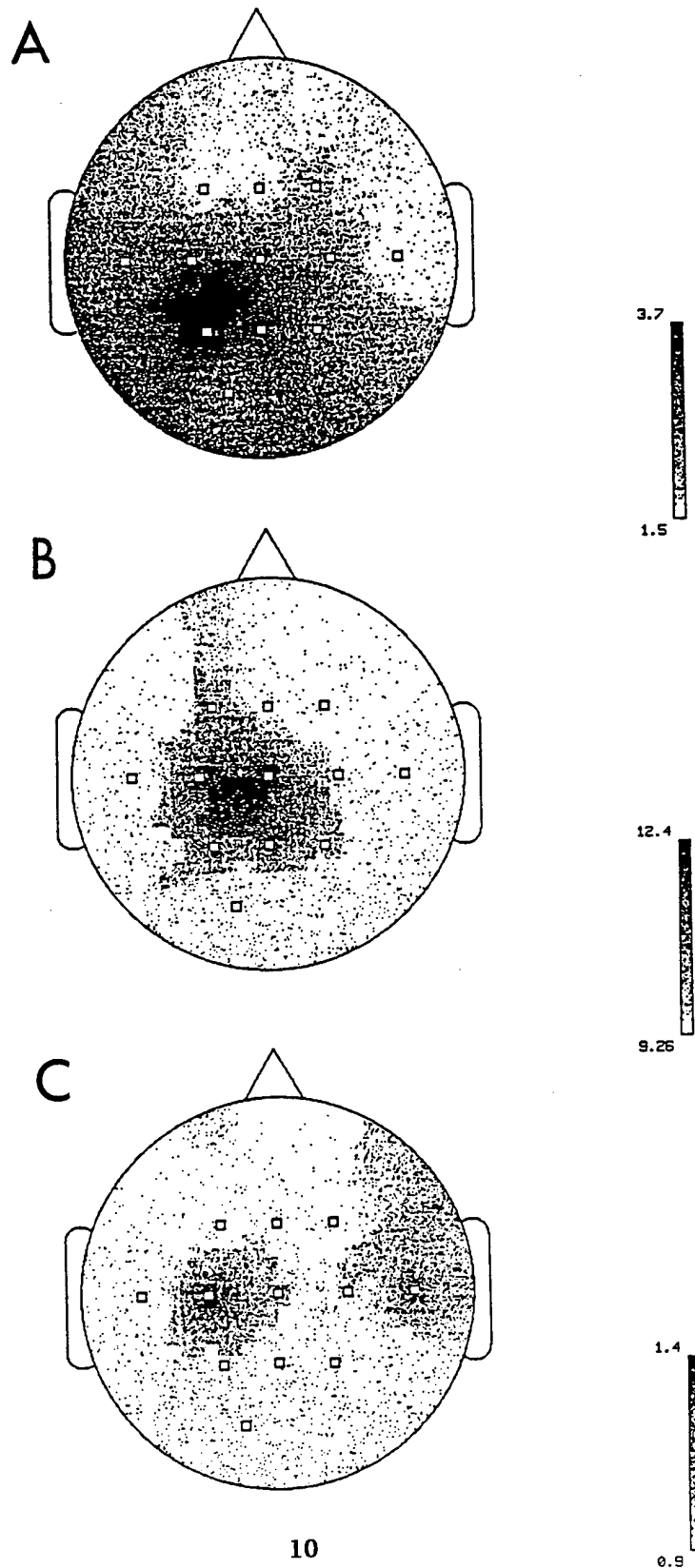
**Figure 2.** Scalp distribution of time-domain evoked responses to one stimulus per ten seconds. Averaged responses for 3 runs each from subjects 1 and 2. TIME axis is 1000msec (200msec of prestimulus), and the vertical bar indicates the time of stimulus onset. The height of the AMPLITUDE axis is 5  $\mu$ V in each direction. The channels displayed are (from left to right): (top row) F3, Fz, F4; (second row from top) T3, C3, Cz, C4, T4; (third row from top) P3, Pz, P4; (bottom row) O1. The electrooculographic recording is plotted at the lower left.



**Figure 3.** Scalp-recorded activity evoked by one stimulus per second. Averaged responses for 13 runs from 5 subjects (N=3975 epochs). Plot shows 170msec of prestimulus activity. Stimulation was presented to the right index fingertip. Channels are labeled according to conventional placement standard described by the International 10/20 System.



**Figure 4.** Topographic maps of positive peaks at approximately 50 and 250 msec. Each plot reflects the base-to-peak amplitude of a given peak at a time point at which its amplitude is maximal in channel C3. The plots were generated using linear interpolation. Each small square marks one of the International 10/20 System sites at which responses were recorded, organized as described in Figure 2 legend. For 1/10 sec condition, data is the same as that used for Figures 1 and 2, and scalp topographies are presented for peaks at 50 msec (A) and 250 msec (B). For the 1/sec condition, data is the same as that used for Figure 3, and topography of the 250-msec peak is shown (C). The calibration bars are in  $\mu V$ .



## *Steady-state Responses*

### General features of the time-domain evoked response

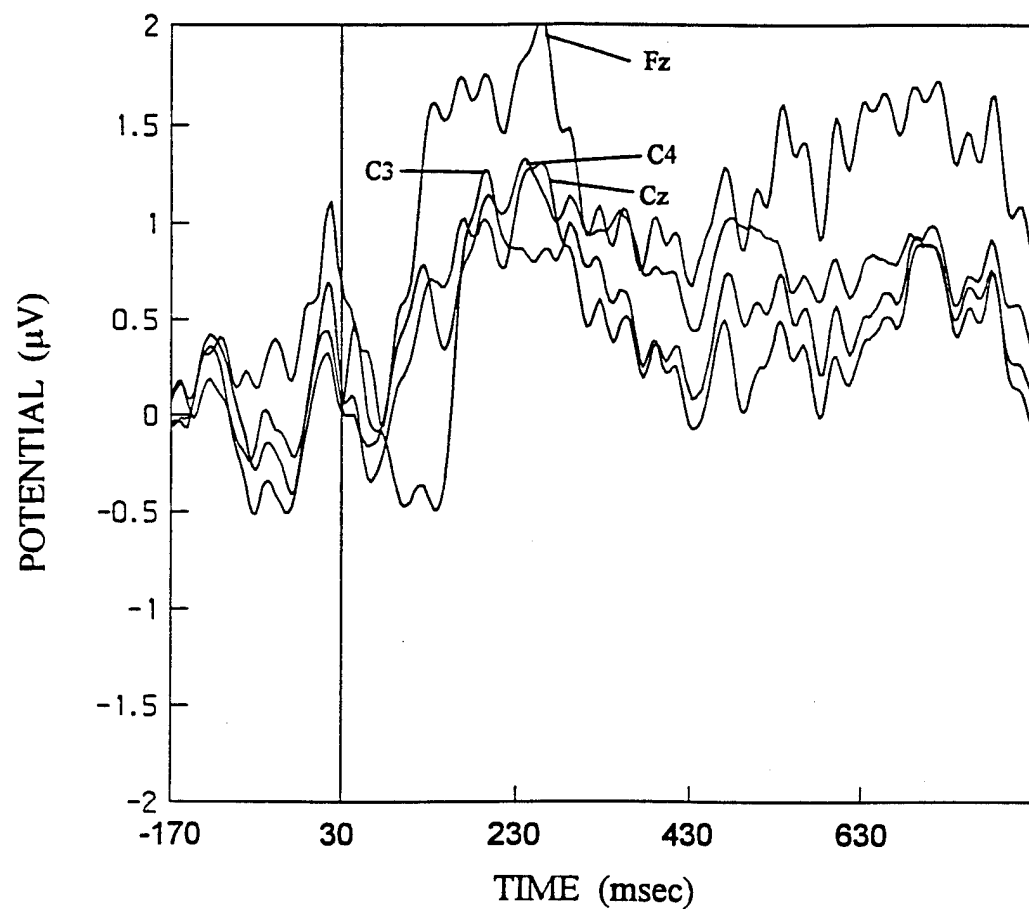
As described in the Methods section, epochs obtained in the rapid-rate conditions were associated with augmentation of the amplitude of single pulses within the ongoing stimulus stream. The response evoked by this stimulus perturbation is shown in Figure 5. Response components evoked in this manner are considerably less distinct than those elicited by the 1/10 sec stimulation rate. Furthermore, the resulting scalp distribution conforms less well to expectation. The poorly defined response components are further obscured by superposition of responses entrained at the frequency of stimulation, approximately 16 cycles in a 500-msec period, confirming response entrainment to 32.5 Hz stimulation. Nonetheless, it is evident that the conventional time-domain negative and positive peaks—which are elicited by perturbations that occur, on average, about 1.5 times per second—have base-to-peak excursions that are on the order of those shown in Figure 3 for the 1/sec presentation rate.

Fourier analysis was used to obtain a measure of the degree of response entrainment to the stimulus frequency. Using this approach, the amplitude of the response was obtained over the course of the run. During stimulation, response levels appear to fluctuate about a mean amplitude, with a cycle length that varies between 20-40 sec (Figure 6), as suggested by Galambos and Makeig (1988). As shown in Figure 6, oscillations having this period were evident across runs and different subjects. Furthermore, characteristic cycle lengths appear for each subject which are maintained across runs. This periodicity is not related to fluctuations in the voltage delivered to the stimulator coil, which is under computer control and is constant throughout the run.

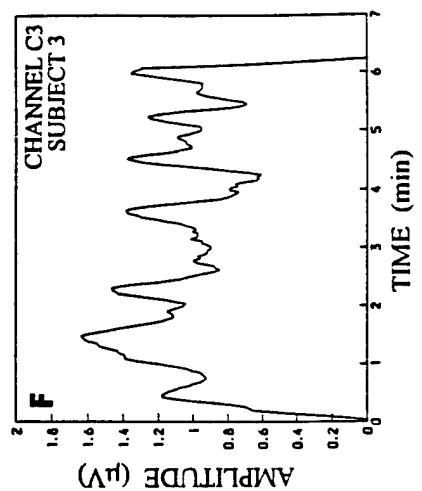
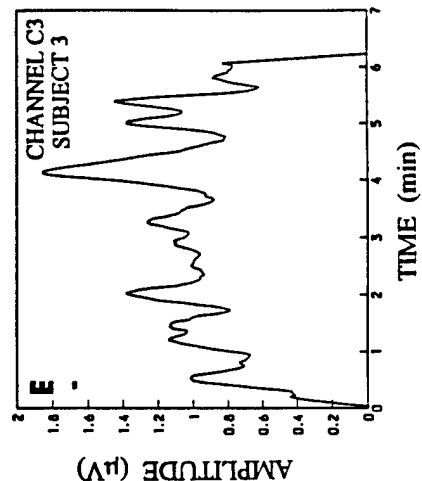
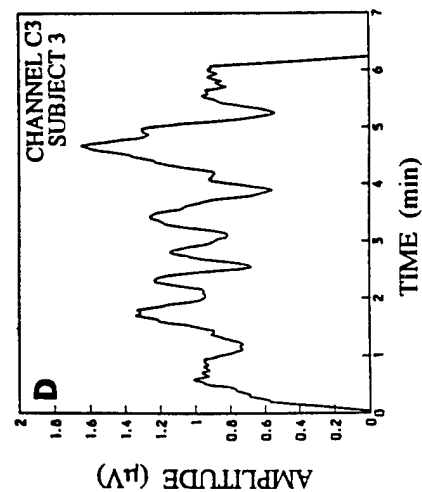
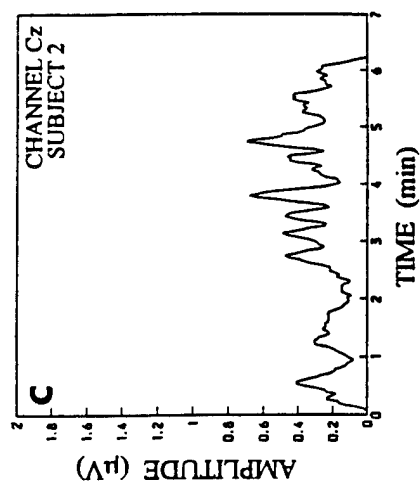
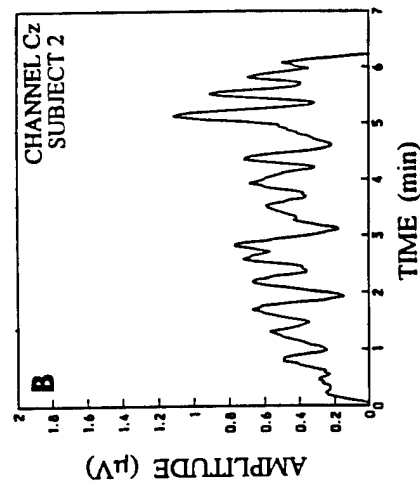
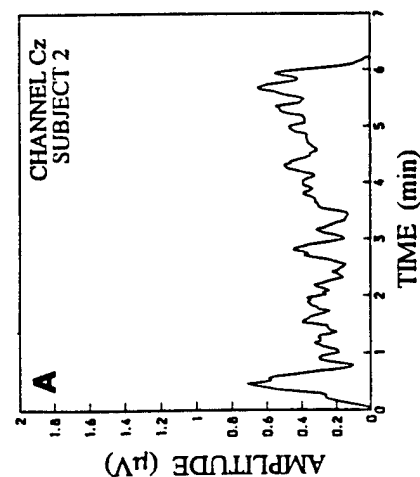
### Topography

Responses entrained to 32.5 Hz were clearly spatially organized. As shown in Figure 7, the amplitudes of responses to 32.5 Hz stimulation were largest at electrodes overlying contralateral somatosensory cortex. Parts A and B show that the pattern of response is readily reproducible for the same subject across sessions. The response is most spatially localized in subject 4 (Figure 7C). The differences in the response distributions across subjects may reflect differences in the morphology of the postcentral gyrus, particularly differences in the orientation of area 3b, the principal receiving area of the primary somatosensory cortex. Furthermore, the highly-localized appearance of the response reduces concern about the possibility that stimulus artifact could have been injected into the physiological responses via transmission through the auditory pathways, or that the electromagnetic field of the stimulator could have contaminated physiological responses detected at the scalp leads.

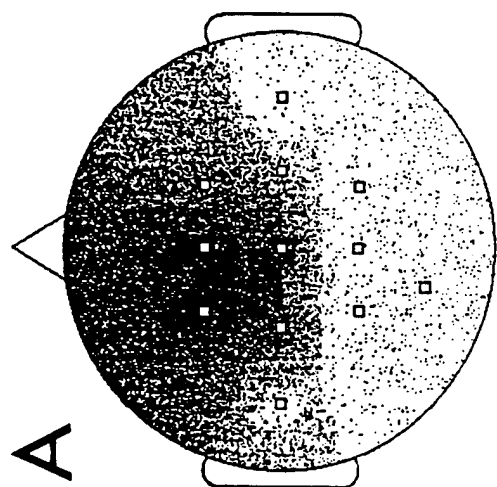
**Figure 5.** Scalp-recorded activity evoked by enhancement of a single pulse within a continuous stimulus train. Enhancements occur at a mean rate of 1.5/sec. Averaged responses for 23 runs from 5 subjects (5924 epochs). The rapid-rate stimulus is continuously presented throughout the run. Plot includes averaged data for 170msec of the prestimulus period. Stimulation was presented to the right index fingertip. Channels are labeled according to conventional placement standard described by the International 10/20 System.



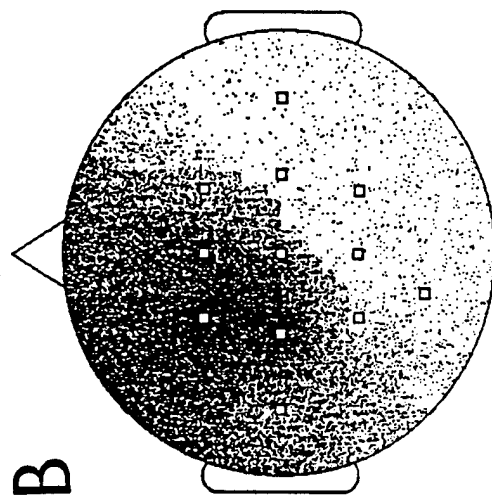
**Figure 6.** Within-run response amplitudes to continuous stimulation at 32.5 Hz. Averaged data for each of 3 runs on two subjects. Responses for channel Cz from subject 2 are in plots A, B, and C; those for channel C3 from subject 3 are presented in D, E, and F. The plot was derived by moving a rectangular averaging window eight epochs long through the individual averages whose amplitude had been determined using Fourier analysis. That is, the first amplitude point gives a moving average for epochs 1 through 8, the second point for epochs 2 through 9, etc.



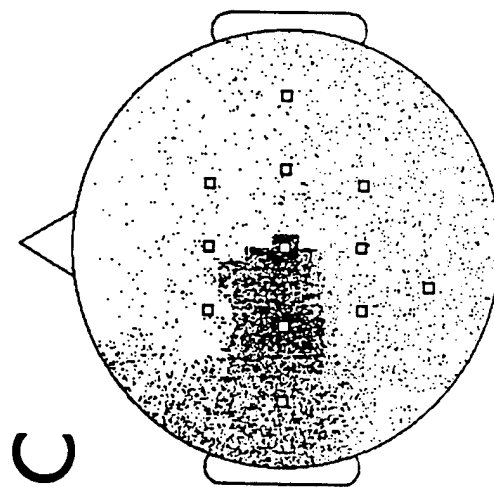
**Figure 7.** Topographic maps of responses to 32.5 Hz stimulation. Amplitude measurements obtained by Fourier analysis as described in the Methods section. The amplitude of the entrained activity is plotted for two sessions from subject 3 (A and B), and for one session from subject 4 (C). The plots were generated using linear interpolation. Each small square marks one of the International 10/20 System sites at which responses were recorded, organized as described in Figure 2 legend. Calibration bars are in  $\mu V$ .



SUBJECT 3



SUBJECT 3



SUBJECT 4

This highly localized distribution is further exemplified by data obtained to simultaneous stimulation of three digits of the hand. Figure 8 shows the spatial organization for both amplitude and phase of the entrained response to 39-Hz stimulation for subject 5. Both measures reflect an anterior parietal activity focus over contralateral scalp.

### Spectral Analysis

Responses to the 32.5 Hz stimulation, transformed into the frequency domain, are shown in Figures 9 and 10. Spectra derived from the mean evoked response averaged across five subjects for channels C3 and Cz reveal clear spectral peaks at the driving rate of 32.5 Hz (Figure 9). Plots of channels C3 and Cz for subject 3 are shown in Figure 10. For subject 3, pronounced spectral components occur at both the stimulus input rate and its second harmonic (65 Hz).

## DISCUSSION

### *General Observations*

Our results are consistent with findings from a number of existing human SEP studies, and serve to considerably extend this body of literature. Our main findings are: (1) Physiological responses to localized tactile stimulation (index finger tip) are maximal over somatosensory-specific scalp regions; (2) Responses to the slowest rate (1/10sec) yield the largest response amplitudes, in accordance with results from several other studies (Angel et al. 1985, Gjerdingen and Tomsic 1970; Hamalainen et al. 1990; Hari 1980; Hashimoto et al. 1988; Hay and Davis 1971; Huttunen and Homberg 1991; Kekoni et al. 1992; McLaughlin and Kelly 1993; Rothman et al. 1970); (3) Neuronal activity driven by moderate intensity tactile stimuli repeated at rapid rates (32.5 or 39Hz) can be detected in scalp recordings using either time- or frequency-domain analyses; (4) The topography of the driving response is reproducible across sessions; (5) Physiological responses contain both first and second harmonics, consistent with cortical single-neuron recordings in monkey (Mountcastle 1984) and with results of other human studies (McLaughlin 1994; Snyder 1992); and (6) Entrained responses exhibit a reproducible fluctuation in amplitude over the course of stimulation, having cycle lengths in the 20-40 sec range, as observed previously by Galambos and Makeig (1988).



**Figure 8.** Topographic maps of the amplitude and phase of the response to a 39-Hz stimulus, delivered to the tip of three fingers (index, middle and ring fingers) of the right hand of subject 5 by a 6.3-cm flat disk connected to the driving coil of the stimulator. Response amplitude (in  $\mu\text{V}$ ) and phase (in degrees) for each channel are plotted for the average of five runs. See Figure 7 legend for further details.

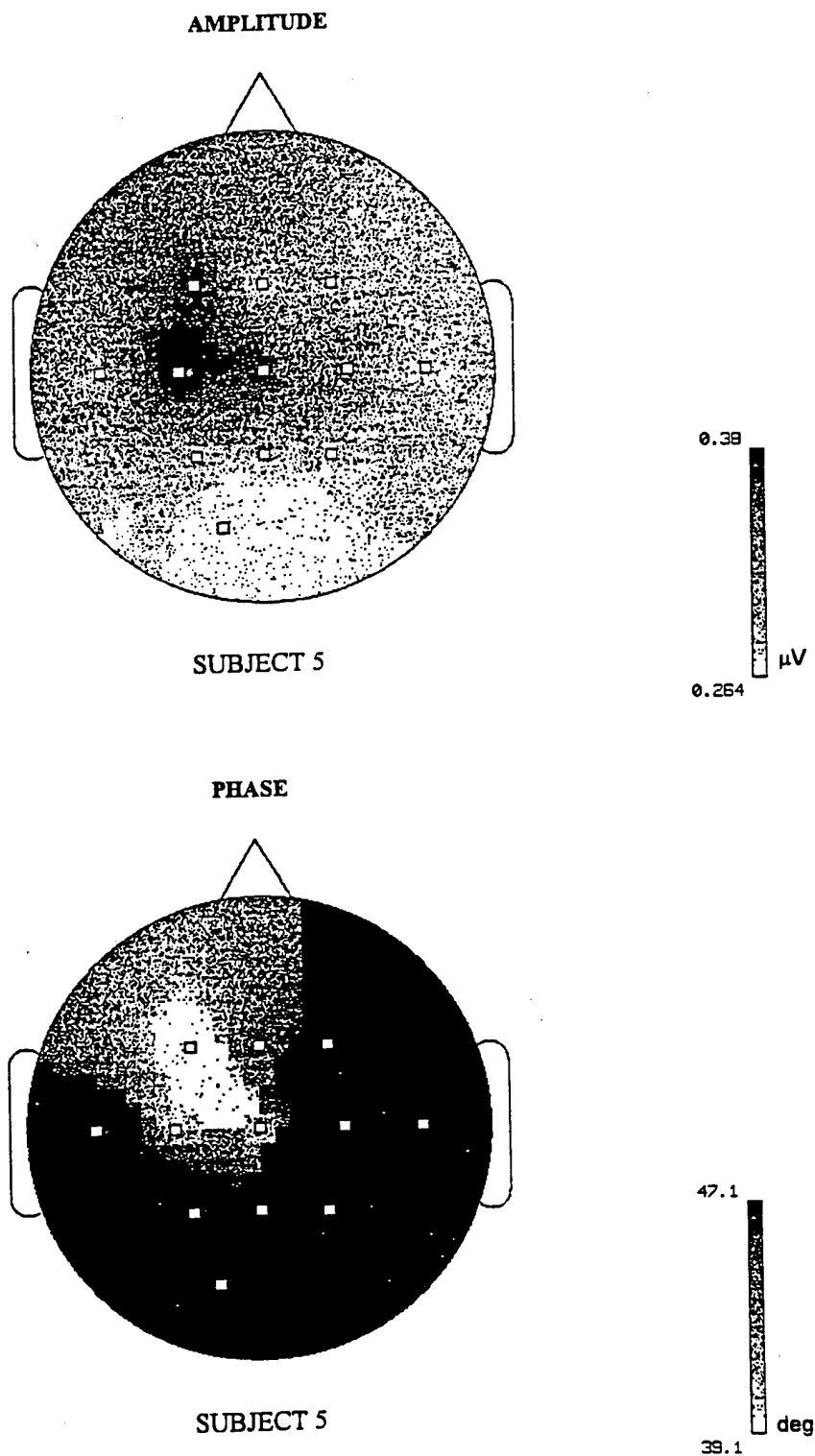


Figure 9. Spectral plots of the unsmoothed grand mean evoked response average of 23 runs from five subjects. Spectra of evoked responses elicited by 32.5 Hz stimulation of the right index fingertip with the 4-mm probe is shown for channels Cz and C3. Arrows mark the fundamental driving frequency. The unsmoothed time-domain data are shown in the insets. Spectral components unrelated to the stimulus frequency reflect spectral estimates of background EEG activity.

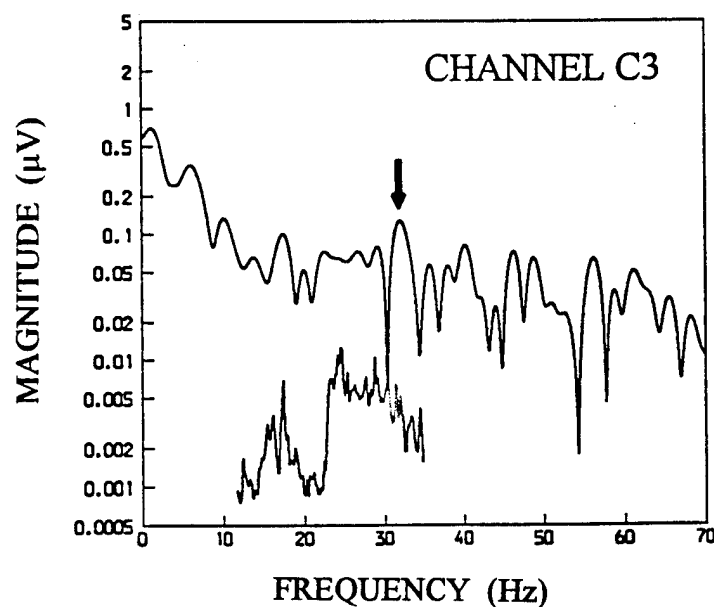
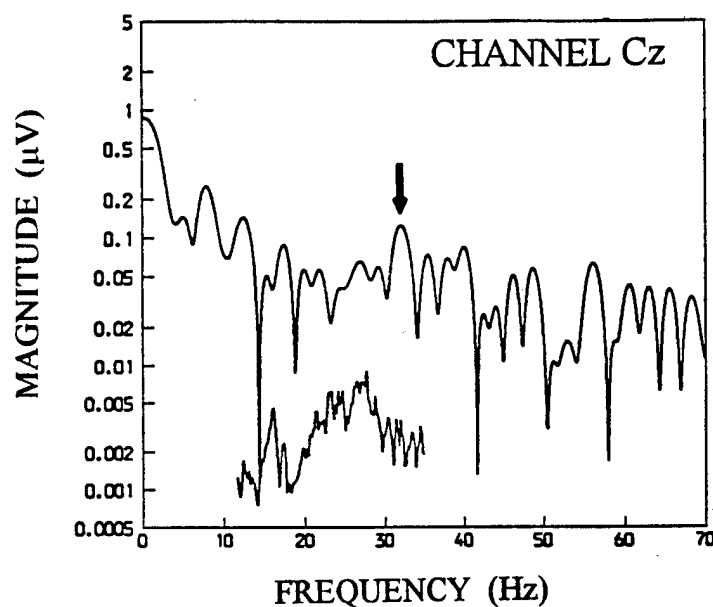
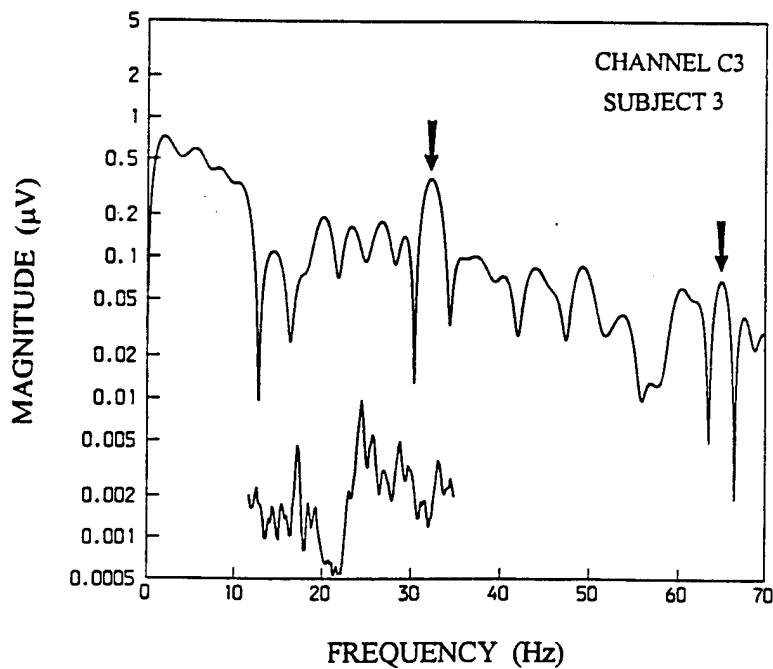
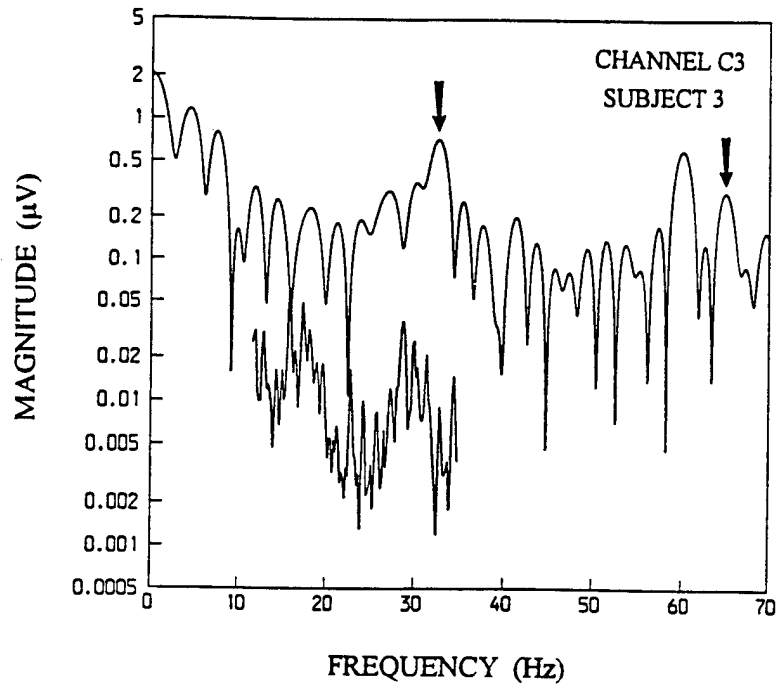


Figure 10. Spectra of unsmoothed evoked responses (insets) recorded during 32.5-Hz stimulation to the right index fingertip with the 4-mm probe. Average of two separate sessions for subject 3 are shown. Arrows mark the fundamental and second harmonic. Line frequency contamination at 60Hz is also evident. See Figure 9 for further details.



### *Time-Domain Evoked Response Components*

Somatosensory evoked response components with latencies longer than 40 msec have been examined by a number of researchers. These studies have employed either electrocutaneous stimulation to the digit and wrist or tactile stimulation of the skin. For both modes of stimulation, scalp recordings obtained near C3, P3 and Cz have been shown to contain response waveforms with similar morphology. Allison et al. (1992) compiled a list of the long-latency components that typically appear following activation of afferents in the median nerve. In scalp recordings, these components are labeled as: P50, N70/P70, N60, P100, N120, P120, N140 and P190. Components P45 (or P50), N60, P100, N140 and P190 have also been reported in several other studies (Desmedt and Tomberg 1989; Franzen and Offenloch 1969; Gjerdingen and Tomsic 1970; Hamalainen et al. 1990; Hari 1980; Hashimoto et al. 1988; Hay and Davis 1971; Huttunen and Homberg 1991; Johnson et al. 1975; Josiassen et al. 1982; Kekoni et al. 1992; Lavine et al. 1980; Michie et al. 1987; Rothman et al. 1970).

In accordance with these studies, our data contain components P50, N140 and P190. The localization of a positivity near 50 msec to posterior parietal scalp (Figure 2) bears striking resemblance to the scalp distribution of component P50 of Allison et al. (1992; see their Figure 2), who suggest that this activity peak reflects activity in area 1 of the primary somatosensory cortex. On the other hand, components N140 and P190 are maximal near the vertex (Cz), as also suggested by our data. These later peaks are thought to reflect activity in frontal cortex (Allison et al. 1992), a claim supported by a clear polarity inversion across cortical laminae within this latency range, and the absence of these peaks in intracranial recordings in the parietal regions. They note, however, that intracranial recordings were confounded by intraoperative procedures such as use of anesthesia and by the passive condition of the subjects. Indeed, later components have been found to change systematically with the arousal state of the subject (Desmedt and Tomberg 1989; Josiassen et al. 1982; Michie et al. 1987), which suggests that late somatosensory components are generated by cognitive processes, presumably in frontal cortex (Allison et al. 1992).

### *Steady-state Responses*

Two key features of the results obtained at the two rapid rates (32.5 and 39Hz) are (1) the clear appearance of response entrainment at the stimulus frequency and (2) the localization of the response to regions of scalp overlying somatosensory cortex. Time-domain and frequency-domain data revealed evidence of an SSR clearly entrained at the frequency of stimulation. Spectral plots also indicated that the

second harmonic was present in the data. The finding that the responses have the largest amplitudes at scalp regions overlying the appropriate sensory cortex offers strong evidence that this recorded activity was generated predominantly by neuronal populations in underlying cortex. Localization to this region was further supported by the scalp distribution of SSR phase. Similar scalp topography was observed by Snyder (1992) who reported that the largest potential gradients occurred between the frontal and parietal regions contralateral to the stimulated hand. Using inverse dipole modeling, Snyder (1992) found that the proposed neural generators lie in or near somatosensory cortex at a location that corresponded to the locus of activity elicited by vibrotactile stimulation of the hand in a regional cerebral blood flow (rCBF) study (Fox et al. 1987).

Little has been done to systematically examine electrophysiologically the frequency-following capacity of the human somatosensory system. In the study by Snyder (1992), tactile stimuli were presented to the palm and finger pads simultaneously at rates ranging from 2 to 40 Hz. Unlike auditory studies, in which maximal response amplitudes near 40 Hz were found, Snyder reported an inversely proportional relationship between response intensity and frequency. One caveat to his results is the absence of test frequencies in the 30-35 Hz range: The highest test frequencies he used were 26 and 40 Hz. Therefore, a study comparable to those performed in audition, addressing the possible optimization of responses at stimulation rates between 20-50 stimuli per second remains to be done.

It is noteworthy to emphasize differences as well as similarities among the topographic distributions of the plots in Figures 7 and 8. We believe that these intersubject differences reflect the unique morphology of the cortical mantle in each subject. The maps for two subjects (Figures 7A, 7B and 8) have frontocentral topographies, whereas topographical organization for a third subject (Figure 7C) largely reflects an activity focus along the mediolateral line connecting C3 and Cz. This difference may simply reflect the position of the postcentral gyrus with respect to the recording sites. Differences in topographic organization may also be due to the orientation of the deep aspects of the central sulcus, along which lies area 3b, the primary receiving area of SI. The latter possibility is consistent with the finding that the anterior and posterior foci of an early 20-msec latency response component--thought to reflect activity in the same area 3b generator--are typically displaced axially with respect to each other. For instance, subjects who have a medially located frontal component have been observed to show a laterally displaced parietal counterpart (Larrea et al. 1992). Furthermore, in cortices where the neural generator is located relatively superficial, the frontal and parietal components appear as a more restricted focus of activity overlying the central sulcus rather than as two distinct frontal and parietal foci, as in Figure 7C.

In comparison with the extensive efforts that have been devoted to characterization of human SSRs in audition and vision (Regan 1989), relevant somatosensory literature is sparse, and includes studies employing a wide array of stimulation paradigms with divergent aims (McLaughlin and Kelly 1993). Further work is necessary to elucidate the neural generators of the entrained responses, in a

manner comparable to similar efforts in audition (Hari et al. 1989). Electrophysiological responses to stimulation of human skin could then be compared with behavioral results obtained in human psychophysical studies (Gescheider and Wright 1968; Goble and Hollins 1993; Hahn 1968; Hollins et al. 1990), and with somatosensory cortical response dynamics reported in animal studies (Mountcastle 1984; Whitsel et al. 1989). We conclude that although these data provide a glimpse of dynamic processing in the human somatosensory system to localized stimulation of the skin, further research is warranted.

#### Acknowledgements

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